

## High soil carbon efflux rates in several ecosystems in southern Sweden

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Soil C effluxes were measured at five forest stands with different vegetation and a meadow in southeastern Sweden (57°5′N, 16°7′E). Exponential regressions of soil respiration against air and soil temperatures were used to model soil respiration at forests stands. For the meadow, a light response curve with gross primary production (GPP) against PAR and a cubic regression with GPP against air temperature were used to model GPP. Soil water content limited soil respiration in all ecosystems but spruce where the limitation appeared only at high soil water content. In the forest ecosystems, the forest floor vegetation was scarce and its C uptake had no significant effect on soil C effluxes. Annual soil respiration in all sites was between 2.05 and 4.34 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup>, which is large as compared with that reported in many other studies. Annual GPP of meadow was between 1.81 and 1.99 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup>, which gives a NEE between 1.39 and 2.41 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup>, i.e. a significant loss of C.

### Introduction

Since 1860 the average temperature on Earth has increased by 0.8 °C and the increase has most likely been caused by human emissions of greenhouse gases, among them CO<sub>2</sub> which contributes most to the radiative forcing (IPCC 2001). Future climate scenarios produced by a range of different global climate models show an increase in average global temperature by 1.4–5.8 °C and changes in precipitation patterns at the end of the 21st century. Concerns about the climatic changes have increased the need for data, information and comprehension of the global C cycle.

Global C budget studies have indicated that a large amount of CO<sub>2</sub> is absorbed by terrestrial

ecosystems (Tans *et al.* 1990). Boreal and temperate forests of the northern hemisphere are especially important for the future development of global climate and today about 50% of the C from fossil fuel emissions is taken up by these forests (Ciais *et al.* 1995). Boreal and temperate forests have a large soil organic C pool (Denning *et al.* 1995) and the largest increase in air temperature is expected at high latitudes (IPCC 2001). Concerns have been expressed that the boreal and temperate forests can change from being C sinks to become C sources (Kirschbaum 1995).

In the study of the C cycle, forests have been in focus due to their large productivity while grasslands have received less attention and this has resulted in lack of data for grassland ecosystems (Valentini *et al.* 2000, Novick *et al.* 2004).

Approximately 40% of the world's terrestrial surface (excluding Greenland and Antarctica) consists of grasslands which form a significant part of the global C cycle as well (White *et al.* 2000, Lecain *et al.* 2002). Most grasslands are grazed and it is, therefore, important to understand the C cycle of meadows (Lecain *et al.* 2002).

Carbon stored in the soil can be released through soil respiration and, according to Kirschbaum (1995), this process is especially vulnerable to global warming. Soil respiration represents between 60% and 80% of the total forest ecosystem respiration (Kelliher *et al.* 1999, Granier *et al.* 2000, Janssens *et al.* 2001b) and it is therefore an important part of the total C exchange between ecosystems and the atmosphere.

During the hours of daylight, gross primary production (GPP) of the ground vegetation can reduce the soil C effluxes. Some studies show that the influence of ground vegetation photosynthesis can be extensive (Goulden and Crill 1997, Law *et al.* 1999a, Morén and Lindroth 2000, Janssens *et al.* 2001a, Widén 2002) while others indicate that the uptake is negligible due to the structure of ground vegetation and regulation of environmental factors (Baldocchi *et al.* 1997, Kelliher *et al.* 1999).

Soil respiration is the sum of respiration from ground vegetation, roots, rhizosphere, mycorrhiza and microbes. There are many different factors that control soil respiration but especially temperature, and sometimes moisture, is a dominant factor (Lloyd and Taylor 1994, Kirschbaum 1995, Davidson *et al.* 2000, Morén and Lindroth 2000, Swanson and Flanagan 2001). The temperature sensitivity varies in different temperature ranges (Kirschbaum 1995) and for the different soil respiration components (roots, microbes, etc.) (Boone *et al.* 1998, Janssens *et al.* 2003). Temperature and respiration of the different components fluctuate seasonally and the temperature sensitivity differs accordingly (Rayment and Jarvis 2000, Widén 2002). GPP is strongly controlled by abiotic factors of which photosynthetic active radiation (PAR), temperature and soil moisture are the most important ones (Lambers *et al.* 1998).

There were several studies attempting to estimate soil C effluxes with more or less advanced

models (Baldocchi *et al.* 1997, Fang and Moncrieff 1999, Law *et al.* 1999b, Rayment and Jarvis 2000, Adams *et al.* 2004, Novick *et al.* 2004) and a simple model that has been successful, used the response of soil C effluxes to temperature, moisture and PAR to extrapolate occasional soil C efflux measurements (Morén and Lindroth 2000, Widén 2002, Janssens *et al.* 2003, Olsrud and Christensen 2004). Because of their simplicity, empirical models are the most frequently used method to simulate soil C effluxes.

The aim of this study was to investigate one of the critical components of the C cycle of boreal and temperate ecosystems, soil C effluxes. To this end we (1) analysed the influence of abiotic factors on soil C effluxes in forest ecosystems and a meadow in the hemiboreal zone, and (2) we tested whether regression equations with C exchange against abiotic factors can be used to model soil C effluxes over an annual cycle.

## Materials and method

### Site description and setup

The investigation took place in March 2004–March 2005 at six sites in the Simpevarp investigation area situated 25 km north of Oskarshamn in southern Sweden (57°5'N, 16°7'E). The mean annual temperature the study year was 7.4 °C, with the highest average monthly temperature of 17.8 °C in August, and the coldest month being February with –1.4 °C. The growing season (threshold 5 °C) started on 15 March and ended on 31 October 2004. The area contains a large variety of ecosystems, but the dominating ones are coniferous forests, deciduous forests and cultivated land.

Six representative ecosystems were used in this study, a pine stand (pine), a spruce stand (spruce), a lichen rock (lichen), two different oak stands (oak 1 and oak 2) and a meadow (meadow). The lichen rock is a coniferous forest ecosystem since the rock is covered with mixed pine and spruce trees. The basic characteristics of the investigated ecosystems are given in Table 1.

A homogeneous area within each ecosystem was divided into nine equally large plots. Within each of these plots, a place for soil C efflux

measurements was selected randomly. In cases when there were branches or obstacles on the ground, which prevented soil C efflux measurements, these were removed.

# Soil C efflux measurements

The soil C efflux measurements were made on 14 occasions over the study year and they were made during the hours of daylight, but started in the morning and ended in the afternoon at different times depending on when the sun rose and set. The measurements were done at exactly the same places all 14 times in all ecosystems but meadow, where marker sticks could not be left in place because of grazing animals. In February and March 2005 some places could not be found due to the snow cover and in these cases a random place in the vicinity was chosen instead. Lichen was not measured in March 2004 and spruce was not measured in January 2005 because of bad weather conditions.

Soil C effluxes were measured using the closed chamber technique. An infrared gas analyzer (EGM-4) together with a canopy assimilation chamber (CPY-2) from PP-systems was used (PP-systems, Hitchin, Hertfordshire, UK). The CPY-2 is a circular transparent chamber with a diameter of 150 mm. The intake to the gas analyzer is located along the circular rim in the form of a copper tubing with small holes distributed along it to ensure representative sampling. In addition, a small fan is also located inside the chamber to help mix the air. The chamber has a sharp rim that was firmly pressed into the humus layer when measurements were taken. This was done carefully in order to avoid disturbance to the soil. The concentration of CO<sub>2</sub> was checked during the measurements and on no occasion could any unprecedented raise in concentration be seen that could be related to the small soil disturbance caused by the insertion of the rim into the humus. The change in concentration of CO<sub>2</sub> in the chamber was continuously measured either for four minutes or when the difference in concentration of CO<sub>2</sub> had changed by 50 ppm. Soil respiration was measured directly afterwards by taking a new measurement but this time the chamber was darkened with a lightproof

**Table 1.** Characteristics of the ecosystems. LAI is maximum leaf surface area per ground surface area divided by two, and green biomass is autumn ground layer green biomass. Soil texture and soil type were taken from Lindborg (2005), total carbon content and humus layer were taken from Lundin *et al.* (2004), basal area, tree height, stand age and LAI were taken from Tagesson (2006b) and litter and green biomass were taken from Löfgren (2005).

Ecosystem	Soil texture	Soil type	Litter (kg d.w. m <sup>-2</sup> )	Total carbon (kg C m <sup>-2</sup> )	Humus layer (cm)	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Tree height (m)	Stand age (yr)	LAI	Green biomass (g dry weight m <sup>-2</sup> )
Pine	Gravel moraine	Regosol, Podzol, Leptosol	—	20.3	16	21.0	19.6	96	3.20	—
Spruce	Clay moraine	Histosol	1.60 ± 1.08	48.7	44	15.5	21.0	55	3.58	8 ± 7
Lichen	—	—	1.22 ± 0.54	—	10	22.5	—	—	3.47	41 ± 22
Oak 1	Sandy moraine	Umbrisol, Regosol	0.49 ± 0.17	6.3	21	15.0	17.1	112	1.55	88 ± 26
Oak 2	Sandy, silty moraine	Umbrisol, Regosol	—	12.8	24	19.5	19.4	133	4.63	—
Meadow	Sandy, silty moraine	Umbrisol	0.48 ± 0.45	27.6	28	—	—	—	—	156 ± 65

hood. The chamber was flushed for fifteen seconds between the measurements to clean it of  $\text{CO}_2$ . The difference between the results of the measurements taken in light and dark conditions is the photosynthesis of the vegetation and, to estimate GPP for the ground vegetation, the soil respiration measurement was subtracted from the soil C efflux measurements.

The chamber was not equipped with any device for pressure regulation. We believe that the soft and porous humus layer functioned as a pressure mediator; if there were any pressure deviations relative to the ambient one, it would most likely be a slight overpressure that would result in a small outflow of air through the humus layer under the rim. An overpressure would result in an underestimation of fluxes and this was not a concern in this study (cf. below).

During the soil C efflux measurements, air temperature, soil temperature, soil moisture and PAR were also measured. Sensors in the CPY-2 chamber measured the air temperature and PAR (PP-system, Hitchin, Hertfordshire, UK). The soil temperature was measured at a depth of 10 cm with a STP-1 sensor (PP-system, Hitchin, Hertfordshire, UK). The soil moisture in the humus layer was also measured over a depth interval of 0–7 cm with a moisture meter (Delta-T devices, Cambridge, UK (HH2-moisture meter with a Theta probe, type ML2X)). The soil type was set to organic. At each plot, three soil moisture measurements were taken and the median value was calculated.

The EGM-4 used in this study had problems with overestimations of soil C effluxes and the data were, therefore, adjusted according to Tagesson (2006a).

## Statistical methods

### Soil respiration

Statistical analyses were carried out with SPSS 12.0.1 for Windows. The results of the regressions were significant if  $p < 0.05$  and insignificant if  $p > 0.1$ ;  $0.05 \leq p \leq 0.1$  indicated a trend relationship.

All soil respiration ( $R_{\text{soil}}$ ) values were allocated into three seasons; the first half of the

growing season (15 March–14 July), the second half of the growing season (15 July–31 October) and winter (1 November–14 March). A one-sample Kolmogorov-Smirnov test was performed to check if  $R_{\text{soil}}$  was normally distributed. For most ecosystems and seasons  $R_{\text{soil}}$  was not normally distributed, but it was after a logarithmic transformation ( $\ln R_{\text{soil}}$ ). 1.9% of the  $R_{\text{soil}}$  values equaled 0 or were negative, hence they were excluded to enable the use of logarithmic transformation.

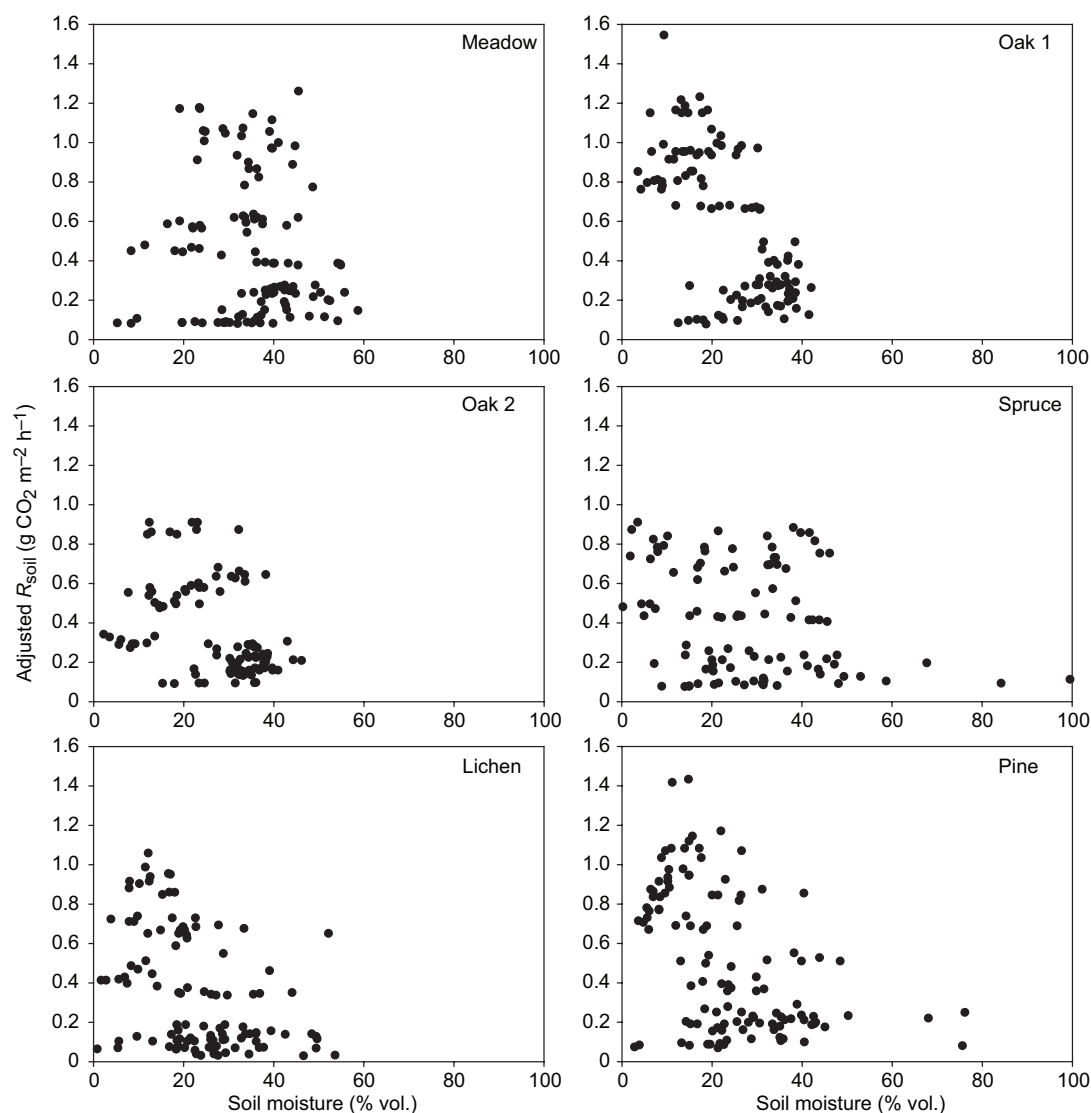
For the seasons, linear regressions of  $\ln R_{\text{soil}}$  against air temperature ( $T_{\text{air}}$ ) and soil temperature at 10-cm depth ( $T_{10\text{cm}}$ ) were calculated. There were problems with the thermometers on 5–6 July 2004, 14–16 February 2005 and 8–10 March 2005, and in total 13.6% of the  $T_{\text{air}}$  and 3.9% of the  $T_{10\text{cm}}$  measurements were excluded. To get results with normal  $R_{\text{soil}}$  instead of in logarithmic values, the linear regressions with  $\ln R_{\text{soil}}$  were rearranged to exponential regressions with normal  $R_{\text{soil}}$ :

$$R_{\text{soil}} = e^{(kT)} \quad (1)$$

where  $T$  is  $T_{\text{air}}$  or  $T_{10\text{cm}}$ .

$Q_{10}$  gives the relative increase in  $R_{\text{soil}}$  when temperature increases by 10 °C and it is an estimate of the effect of temperature on  $R_{\text{soil}}$  in the temperature range within which the measurements were made.  $Q_{10}$  for  $R_{\text{soil}}$  was calculated as  $Q_{10} = e^{10k}$ , where  $k$  is taken from Eq. 1 with  $R_{\text{soil}}$  against  $T_{10\text{cm}}$ .

To analyze the dependence of  $R_{\text{soil}}$  on soil moisture, we first adjusted  $R_{\text{soil}}$  to field measured  $T_{10\text{cm}}$  using Eq. 1 with  $R_{\text{soil}}$  against  $T_{10\text{cm}}$ ; we hereby reduced the effect of temperature. The soil moisture did not have any direct effect on  $R_{\text{soil}}$  but edge effects could be seen (Fig. 1). To analyse these edge effects, for each ecosystem a boundary line analysis of adjusted  $R_{\text{soil}}$  against soil moisture was performed. In the boundary line analysis, the adjusted  $R_{\text{soil}}$  values were sorted by soil moisture and separated into ten groups. In the groups, all values above average plus one standard deviation were extracted. A one-sample Kolmogorov-Smirnov test was performed to check whether the extracted values were normally distributed. For all ecosystems they were normally distributed, hence linear regressions



**Fig. 1.** Adjusted  $R_{\text{soil}}$  ( $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) against soil moisture (% vol.) for all ecosystems.

could be used to analyse whether soil moisture had any limiting effect on  $R_{\text{soil}}$ .

### Soil respiration modeling

At Äspö climate station,  $T_{\text{air}}$  is measured every 30 minutes (Lärke *et al.* 2005). To obtain air temperatures for different ecosystems, linear regressions of  $T_{\text{air}}$  measured in the field against  $T_{\text{air}}$  measured at Äspö climate station were calculated. The regression equations were used to

model  $T_{\text{air}}$  for the different ecosystems over the study year. Equation 1 was used for this dataset to model  $R_{\text{soil}}$  for the same period. No model was made for the months where no significant relationship existed; average  $R_{\text{soil}}$  values measured in the field were used instead. Annual  $R_{\text{soil}}$  for the different ecosystems were calculated by adding together the modelled effluxes of every hour of the year. Residuals were calculated by subtracting modelled  $R_{\text{soil}}$  from  $R_{\text{soil}}$  measured in the field at the closest half-hour from the time of when the field measurements were done.

No soil temperature data existed for the entire study year and soil temperature was therefore modelled.  $T_{10\text{cm}}$  was logged in the pine stand every three hours between 24 March and 4 July 2004; daily average  $T_{10\text{cm}}$  was calculated for this period. For the same period, daily average  $T_{\text{air}}$  was calculated from the measurements taken up at Äspö climate station and a linear regression of the calculated daily average  $T_{10\text{cm}}$  against the daily average  $T_{\text{air}}$  was calculated. The regression was then used to model daily average soil temperature ( $T_{a10\text{cm}}$ ) for the study year.

Temperature varies like a wave over the day so to estimate the diurnal variations of  $T_{10\text{cm}}$ , the amplitude of the wave ( $A_0$ ) for every day was calculated by dividing the daily temperature range by two ( $(T_{\text{max}} - T_{\text{min}})/2$ ). This was done both for the logged  $T_{10\text{cm}}$  and for the  $T_{\text{air}}$  measured at Äspö climate station. Regressions with calculated amplitude of the measured  $T_{10\text{cm}}$  against calculated amplitude of the measured  $T_{\text{air}}$  24 March–4 July 2004 were calculated. The growth regression showed the best fit and it was used on the calculated  $T_{\text{air}}$  amplitude to calculate the amplitude of  $T_{10\text{cm}}$ . The diurnal variation was estimated by  $\cos(\omega t + 1.725)$ , where 1.725 was added to adjust for the diurnal time lag between soil and air temperature.  $T_{10\text{cm}}$  was then modelled for the study year by:

$$T_{10\text{cm}}(t) = T_{a10\text{cm}} + A_0[\cos(\omega t + 1.725)] \quad (2)$$

where  $T_{10\text{cm}}(t)$  is the modelled soil temperature at daytime  $t$  (Hillel 1980).

Equation 1 was used with  $T_{10\text{cm}}(t)$  to estimate  $R_{\text{soil}}$  for the study year. Annual  $R_{\text{soil}}$  for the different ecosystems were calculated by adding modelled  $R_{\text{soil}}$  together. Residuals were also calculated with modelled  $R_{\text{soil}}$  subtracted from  $R_{\text{soil}}$  measured in the field at the half-hour closest to the actual time of each measurement.

### Gross primary production, GPP

GPP values measured during the growing season were included in the one-sample Kolmogorov-Smirnov test to check whether they were normally distributed. This was the case for the meadow only. A one-sample  $t$ -test for the

meadow and the Mann Whitney  $U$ -test for the other ecosystems were then performed. It was only in the meadow that GPP had an effect on soil C effluxes and it was therefore only in this ecosystem that the effect of abiotic factors on GPP was analyzed.

To analyse the effect of PAR on GPP, a light response curve was fitted to the GPP data set:

$$\text{GPP} = -(\text{GPP}_i + R_d) \left( 1 - e^{[(-b_1 \text{PAR})/(\text{GPP}_i + R_d)]} \right) + R_d \quad (3)$$

where  $\text{GPP}_i$  is saturated GPP,  $R_d$  is deduced respiration and  $b_1$  is quantum efficiency. Saturated GPP is where GPP levels out, deduced respiration is NEE at zero PAR and quantum efficiency is the initial slope of the curve. Quantum efficiency gives the efficiency of the vegetation to take up PAR.

A commonly used equation to analyse the relationship between GPP and air temperature is the Arrhenius function of temperature (Wang *et al.* 1996, Lankreijer 1998). In this study, a cubic regression was fitted instead because it has the same sigmoidal shape as the Arrhenius function, but it is mathematically easier to work with.

$$\text{GPP} = \text{GPP}_0 + b_1 T_{\text{air}} + b_2 T_{\text{air}}^2 + b_3 T_{\text{air}}^3 \quad (4)$$

where,  $\text{GPP}_0$  is the GPP at 0 °C, and  $b_{1,2,3}$  are coefficients of the regression.

A boundary line analysis was also done to examine if soil moisture had any effect on GPP. Table-curve Windows ver. 1.0 was used to find any significant relationships between soil moisture and GPP.

### GPP modelling for the meadow

At Äspö climate station, global radiation is measured every 30 minutes (Lärke *et al.* 2005). PAR was estimated by taking 0.45 of total global radiation (Monteith and Unsworth 1990). Equation 3 was used to estimate GPP throughout the growing season. The modelled air temperature set for meadow during the growing season was used with Eq. 4 to estimate GPP. GPP was set to zero during the hours of darkness. Annual GPP was calculated by adding the modelled values together and residuals were calculated with mod-



elled GPP subtracted from GPP measured in the field at the closest half-hour from when the field measurements were done.

## Model evaluations

To evaluate the models and calculate the error of the obtained results, the standard deviations were needed. For the regression models without propagation errors in them, standard deviation was calculated in SPSS 12.0.1 and for the models that included several modelled variables; the formula for error propagation was used (Leo 1994):

$$\begin{aligned}\sigma^2(f) = & (\partial f/\partial x)^2\sigma^2(x) + (\partial f/\partial y)^2\sigma^2(y) \\ & + (\partial f/\partial z)^2\sigma^2(z) + (\partial f/\partial a)^2\sigma^2(a) \\ & + 2\text{cov}(x,y)(\partial f/\partial x)(\partial f/\partial y)\end{aligned}\quad (5)$$

where  $\sigma^2(f)$  is variance in modelled result,  $\sigma^2(x)$  is variance of factor in function,  $\sigma^2(y)$  is variance of coefficient in function, the  $\sigma^2(z)$  is variance of variable in function (i.e.  $T_{\text{air}}$  and  $T_{10\text{cm}}$ ),  $\sigma^2(a)$  is variance from correction of soil C efflux measurements and  $\text{cov}(x,y)$  is covariance between the

factors and coefficients in the functions.

The standard deviations of the models were estimated as the square root of the variances. Finally, to evaluate the results of a model, a  $t$ -test was performed where residuals were compared against  $t$  times the standard deviation of the model to see if the field results were within the 95% confidence interval of the model.  $t$  is from Student's  $t$ -test and found in a table of critical values for  $t$  distribution.

## Results

### Effect of air temperature, soil temperature and soil moisture on soil respiration

$T_{\text{air}}$  had a significant effect on  $R_{\text{soil}}$  for all ecosystems and during all seasons, except for pine, oak 2 and meadow during winter (Table 2). Excluding the non-significant cases,  $T_{\text{air}}$  explained on average 30.6% of the variation in  $R_{\text{soil}}$  and at best 56.9% of the variation was explained (lichen, season 3) (Table 2).

$T_{10\text{cm}}$  explained  $R_{\text{soil}}$  better than  $T_{\text{air}}$ . It was significant for all ecosystems and during all seasons

**Table 2.** Parameters of the regression  $R_{\text{soil}} = R_0 e^{kT}$  and statistics for measured soil respiration against the air temperature.  $R_{\text{soil}}$  = soil respiration ( $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ),  $R_0$  = initial soil respiration at  $0^\circ\text{C}$ ,  $T$  = air temperature ( $^\circ\text{C}$ ), d.f. = degrees of freedom.

Ecosystem	Season	d.f.	$R_0$	$k$	$F$	$p$	$R^2$
Pine	1*	32	0.119	0.069	17.1	0.000	0.35
	2**	44	0.490	0.026	5.4	0.025	0.11
	3***	18	0.189	-0.006	0.0	0.913	0.00
Spruce	1*	27	0.051	0.103	15.2	0.001	0.36
	2**	42	0.292	0.043	5.3	0.027	0.11
	3***	26	0.077	0.148	10.3	0.004	0.29
Lichen	1*	23	0.007	0.146	16.6	0.001	0.42
	2**	43	0.209	0.056	12.3	0.001	0.22
	3***	27	0.055	0.194	35.7	0.000	0.57
Oak 1	1*	33	0.089	0.065	6.6	0.015	0.17
	2**	43	0.463	0.040	10.2	0.003	0.19
	3***	36	0.050	0.229	34.0	0.000	0.49
Oak 2	1*	24	0.099	0.027	4.5	0.045	0.16
	2**	42	0.158	0.074	16.8	0.000	0.29
	3***	27	0.085	0.100	1.4	0.254	0.06
Meadow	1*	31	0.148	0.067	33.8	0.000	0.52
	2**	42	0.280	0.046	23.8	0.000	0.36
	3***	31	0.139	-0.022	1.4	0.241	0.04

\* 15 March 2004–14 July 2004, \*\* 15 July 2004–31 October 2004, \*\*\* 1 November 2004–14 March 2005.

**Table 3.** Parameters of the regression  $R_{\text{soil}} = R_0 e^{kT}$  and statistics for measured soil respiration against soil temperature.  $R_{\text{soil}}$  = soil respiration ( $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ),  $R_0$  = initial soil respiration at  $0^\circ\text{C}$ ,  $T$  = soil temperature ( $^\circ\text{C}$ ), d.f. = degrees of freedom.

Ecosystem	Season	d.f.	$R_0$	$k$	$F$	$p$	$R^2$
Pine	1*	35	0.106	0.139	32.0	0.000	0.48
	2**	44	0.176	0.112	25.0	0.000	0.36
	3***	41	0.070	0.210	31.5	0.000	0.43
Spruce	1*	32	0.046	0.191	64.1	0.000	0.67
	2**	43	0.171	0.100	16.1	0.000	0.27
	3***	26	0.071	0.213	21.1	0.000	0.45
Lichen	1*	23	0.004	0.345	41.2	0.000	0.64
	2**	42	0.107	0.126	17.1	0.000	0.29
	3***	36	0.060	0.200	46.0	0.000	0.56
Oak 1	1*	33	0.030	0.228	67.0	0.000	0.67
	2**	43	0.375	0.062	8.6	0.005	0.17
	3***	33	0.079	0.263	97.3	0.000	0.75
Oak 2	1*	33	0.055	0.179	54.6	0.000	0.62
	2**	43	0.085	0.138	18.1	0.000	0.30
	3***	32	0.088	0.142	7.2	0.011	0.17
Meadow	1*	34	0.150	0.137	94.2	0.000	0.74
	2**	42	0.113	0.126	47.2	0.000	0.53
	3***	39	0.077	0.242	36.5	0.000	0.48

\* 15 March 2004–14 July 2004, \*\* 15 July 2004–31 October 2004, \*\*\* 1 November 2004–14 March 2005.

and on average 47.6% of the variation in  $R_{\text{soil}}$  was explained. In the best case,  $T_{10\text{cm}}$  explained as much as 73.5% of the variation (meadow, season 1) (Table 3).

**Table 4.** The relative increase in soil respiration when soil temperature at 10-cm depth is increased by  $10^\circ\text{C}$  ( $Q_{10} = e^{10k}$ ).

Ecosystem	Season	d.f.	$Q_{10}$	Soil temperature range ( $^\circ\text{C}$ )
Pine	1*	35	4.0	2.5–16.0
	2**	44	3.1	9–18.7
	3***	41	8.1	0.3–6.8
Spruce	1*	32	6.7	0.1–15.4
	2**	43	2.7	8.7–16.8
	3***	26	8.4	0.4–6.6
Lichen	1*	23	31.6	6.1–16.4
	2**	42	3.5	9.1–17.6
	3***	33	7.4	0.7–5.7
Oak 1	1*	33	9.7	2.7–17.3
	2**	43	1.9	9.1–19.1
	3***	33	13.9	0.3–7.0
Oak 2	1*	33	6.0	1.3–13.2
	2**	43	4.0	8.5–17.2
	3***	32	4.1	0.3–7.1
Meadow	1*	34	3.9	1.2–15.6
	2**	42	3.5	9.6–18.6
	3***	39	11.3	0.3–5.0

\* 15 March 2004–14 July 2004, \*\* 15 July 2004–31 October 2004, \*\*\* 1 November 2004–14 March 2005.

There was large seasonal variation in  $Q_{10}$ , which generally was larger in the first half of the growing seasons and in winter as compared with the second half of the growing season (Table 4). On average  $Q_{10}$  was 7.4. The largest value (31.6) was found in the lichen ecosystem in the first half of the growing season while it was smallest (1.9) in oak 1 in the second half of the growing season.

Adjusted  $R_{\text{soil}}$  did not follow humus layer soil moisture, and there must therefore be some other factor that affected  $R_{\text{soil}}$ . Visually, it appeared that there was a slight decrease in  $R_{\text{soil}}$  at low soil moisture, while a more pronounced effect could be seen at high moisture (Fig. 1). The highest  $R_{\text{soil}}$  rates occurred at soil moisture values of 15%–20% vol., while the rates dropped to practically zero when soil moisture was between 45% and 60% vol., depending on the ecosystem. Soil moisture reached these high values since measurements were made in the humus layer and not in the mineral part of the soil, and the humus layer has higher porosity than mineral soil. The slight decrease in  $R_{\text{soil}}$  in dry soils was not shown in the boundary line analysis while a linear limiting effect on  $R_{\text{soil}}$ , as the soils were getting wetter, could be seen for all ecosystems but spruce. For spruce, a threshold effect was seen



at about 50% vol. above which  $R_{\text{soil}}$  was strongly reduced (Fig. 1).

### Seasonal and annual soil respiration

A comparison between  $R_{\text{soil}}$  measured in the field and  $R_{\text{soil}}$  estimated by the regression models indicated that they were reasonably close to each other. None of the residuals was outside the 95% confidence interval of the soil temperature modelled  $R_{\text{soil}}$  and for the air temperature modelled  $R_{\text{soil}}$ , it was only oak 2 on the 5 July that was outside the 95% confidence interval. In total, both models underestimated  $R_{\text{soil}}$ , but the soil temperature model showed a smaller underestimation than the air temperature model.

There was a large seasonal variation in modelled  $R_{\text{soil}}$  and both air temperature and soil temperature based models peaked in August. Generally, it took longer for air temperature modelled  $R_{\text{soil}}$  to start up in spring than for the soil temperature model (Fig. 2).

The mean monthly maximum rates of  $R_{\text{soil}}$  peaked in August and they were 1.18, 1.11, 1.00, 0.92, 0.88 and 0.76 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> in pine, oak 1, meadow, spruce, lichen and oak 2, respectively. Pine, oak 1 and meadow showed similar annual respiration with 3.4–4.4 kg CO<sub>2</sub> yr<sup>-1</sup> followed by spruce with 2.4–3.1 kg CO<sub>2</sub> yr<sup>-1</sup>, oak 2 with 2.4–2.9 kg CO<sub>2</sub> yr<sup>-1</sup> and lichen with 2.1–2.8 kg CO<sub>2</sub> yr<sup>-1</sup> (Table 5).

### Effect of PAR, air temperature and soil moisture on GPP in meadow

In the meadow, Eq. 3 explained 32.7% of the variation in GPP (Fig. 3). GPP was satu-

rated at 0.909 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>, the quantum efficiency was 0.003 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> (μmol photons m<sup>-2</sup> s<sup>-1</sup>)<sup>-1</sup> and deduced respiration rate was -0.031 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>. Quantum efficiency was recalculated to 0.019 mol CO<sub>2</sub> (mol photons)<sup>-1</sup>.  $T_{\text{air}}$  affected GPP as well and 33.9% of the variation in GPP could be explained by Eq. 4 (Table 6). The boundary line analysis with GPP against soil moisture indicated that there was no significant effect of soil moisture on GPP.

### GPP in meadow during growing season

The comparison between the model with GPP against PAR and field measured GPP showed fairly good agreement; all residuals were inside the 95% confidence interval of the modelled GPP. In total, the model tended to overestimate GPP. According to this model, the ground vegetation in meadow annually took up 1.99 ± 1.34 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup>.

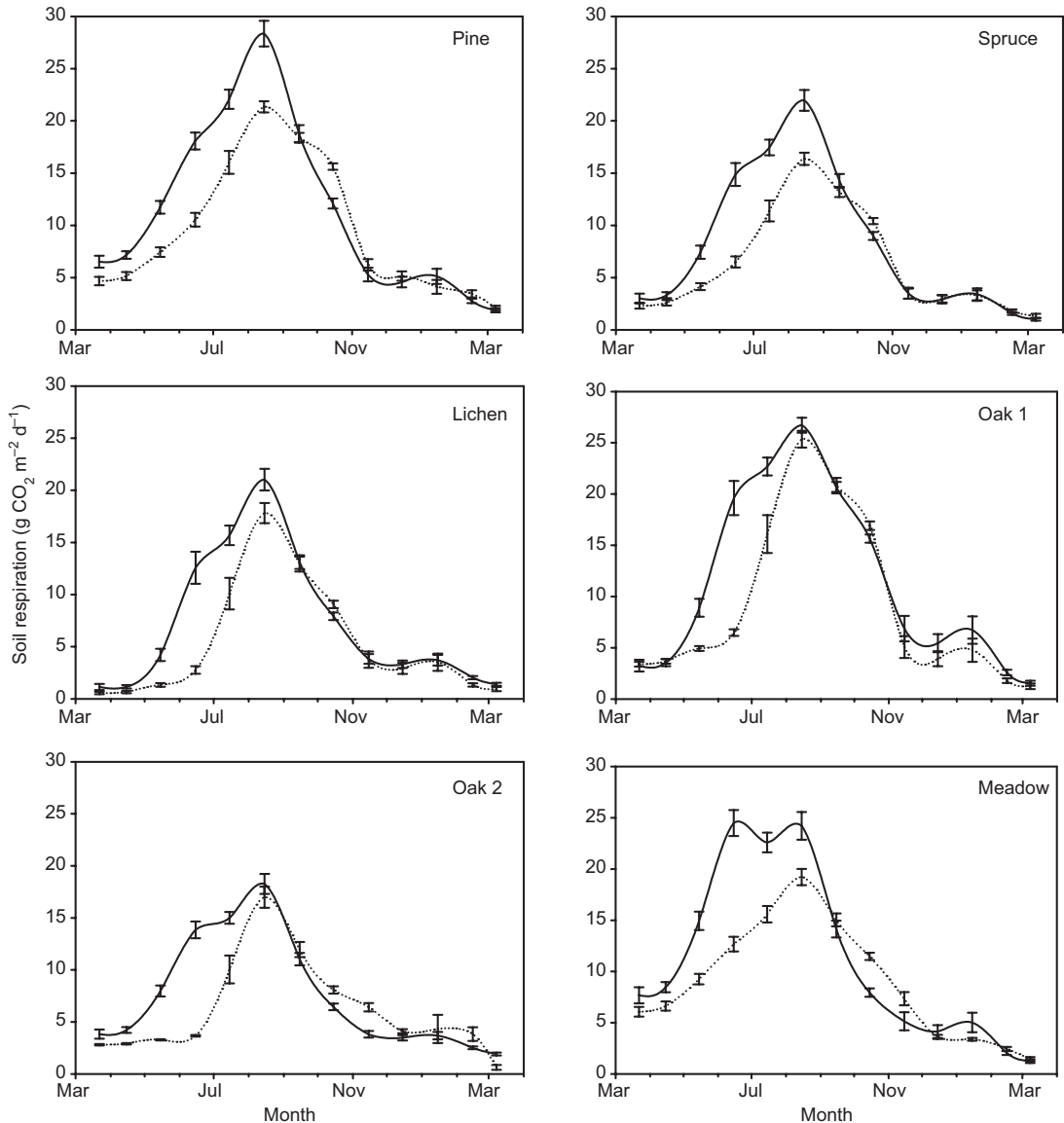
The air temperature model also fitted well with GPP measured in the field and it indicated that 1.81 ± 0.80 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup> was annually taken up by ground vegetation, i.e. slightly less

**Table 5.** Annual soil respiration (15 March 2004–14 March 2005) ± S.D. (kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup>) for the air temperature and soil temperature based models.

Ecosystem	Air-temperature based model	Soil-temperature based models
Pine	3.58 ± 1.19	4.30 ± 1.78
Spruce	2.39 ± 1.17	3.12 ± 1.53
Lichen	2.05 ± 1.32	2.75 ± 2.67
Oak 1	3.44 ± 1.35	4.34 ± 1.87
Oak 2	2.36 ± 1.24	2.85 ± 1.63
Meadow	3.38 ± 1.01	4.22 ± 1.36

**Table 6.** Regression parameters and statistics for the GPP regressions ( $GPP = GPP_0 + b_1 T_a + b_2 T_a^2 + b_3 T_a^3$ ) for the air temperature regression, where  $GPP_0$  = initial GPP at 0 °C and  $T_a$  is air temperature and  $GPP = -(GPP_1 + R_d) \left( 1 - e^{[(-b_1 PAR)/(GPP_1 + R_d)]} \right) + R_d$  for the PAR regression, where  $GPP_1$  is saturation level of GPP,  $R_d$  is deduced respiration and  $b_1$  is quantum efficiency. GPP is in g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> and d.f. is degrees of freedom. PAR is in μmol photons m<sup>-2</sup> s<sup>-1</sup>.

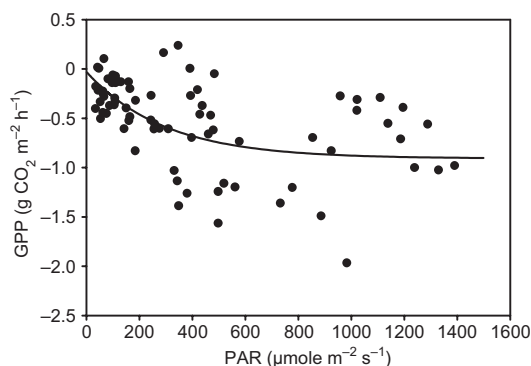
Regression	d.f	$GPP_{0,1}$	$b_1$	$R_d, b_2$	$b_3$	$F$	$p$	$R^2$
Air temperature	73	-0.060	0.001	-0.002	3.3E-05	12.5	0.000	0.34
PAR	79	0.909	0.003	-0.031	-	18.7	< 0.01	0.33



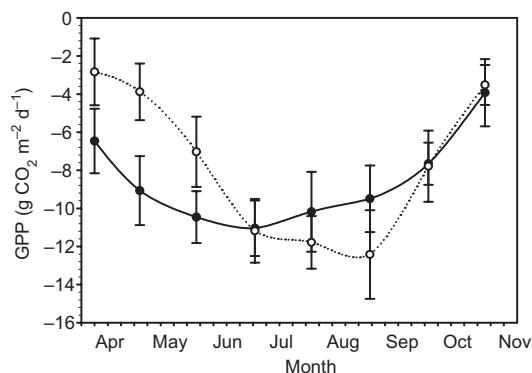
**Fig. 2.** Seasonal variation in monthly average air and soil temperature modelled  $R_{\text{soil}}$  (g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>) for the study year for all ecosystems. The thick line is average monthly soil temperature modelled  $R_{\text{soil}}$  and the dotted line is average monthly air temperature modelled  $R_{\text{soil}}$ . Error bars are one standard deviation of monthly-modelled  $R_{\text{soil}}$ . For air temperature modelled  $R_{\text{soil}}$  in November 2004–March 2005, average measured values were used for pine, oak 2 and meadow, since no significant relationship for  $R_{\text{soil}}$  to  $T_{\text{air}}$  existed.

than the PAR based model. None of the residuals were outside the 95% confidence interval and in total this model estimated GPP well. The seasonal distribution of GPP showed quite different patterns depending on which model was used (Fig. 4). The PAR based model had its maximum in June/July while the temperature-based model

showed a maximum in August. For the meadow, NEE could be calculated since both GPP and  $R_{\text{soil}}$  were estimated and depending on the model, the estimated annual NEE losses ranged between 1.39 and 2.41 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup>, i.e. significant losses of C to the atmosphere.



**Fig. 3.** Response of GPP to PAR. Dots are field measured values and the trend line is the light response curve  $GPP = -(0.909 - 0.031)(1 - e^{[-0.003PAR]/(0.909 + 0.031)}) - 0.031$ .



**Fig. 4.** Monthly average modelled GPP ( $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) for the growing season, in meadow. Solid line is PAR modelled GPP and dotted line is air temperature modelled GPP. Error bars are one standard deviation of monthly-modelled GPP.

## Discussion

### Effect of temperature and soil moisture on soil respiration

Studies made in temperate regions have indicated that the main factor to influence soil respiration is temperature (e.g. Davidson *et al.* 1998, Morén and Lindroth 2000, Swansson and Flanagan 2001), which also could be seen in this study. In some ecosystems in winter,  $T_{\text{air}}$  did not affect  $R_{\text{soil}}$ , which can be explained by inactive vegetation and frozen ground. Inactive vegetation means that autotrophic respiration is low and in frozen ground the main part of soil respiration originates from the deeper parts of the soil (Rayment and Jarvis 2000), which is little affected by shifts in air temperature. Soil temperature, though, has a large impact on soil respiration in this part of the soil.

The parameter  $k$ , from Eq. 1, is not a constant coefficient; it decreases with increasing temperature (Kirschbaum 1995).  $Q_{10}$  therefore differs between the seasons and the second half of the growing season with highest soil temperature, in general, has the lowest  $Q_{10}$ . Average  $Q_{10}$  in Simpevarp was slightly higher as compared with that in many other ecosystems studied, where  $Q_{10}$  at soil depths between 2 and 15 cm ranged from 2.0–6.0 (Goulden and Crill 1997, Boone *et al.* 1998, Davidson *et al.* 1998, Hollinger *et al.* 1998, Morén and Lindroth 2000, Pilegaard *et al.* 2001, Swansson and Flanagan 2001). Some other studies have

shown really large  $Q_{10}$ , Rayment and Jarvis (2000) found  $k$  values between 0 and 0.5, which is the same as  $Q_{10}$  between 0–148, and Widén (2002) found  $k$  values between 0.02 and 1.02, which gives  $Q_{10}$  up to about 27 000.  $Q_{10}$  can differ considerably between different studies. Firstly,  $k$  is temperature-dependent and the studies to be compared must therefore have been performed in the same temperature range. Secondly, it is important that  $Q_{10}$  is derived from soil temperature measured at the same depth in the different studies.  $Q_{10}$  in Simpevarp would have differed greatly if they had been derived from  $T_{\text{air}}$  instead.

Inhibition of soil respiration in drier soils is an effect of desiccation stress while inhibition in more moist areas is a result of the development of anaerobic conditions (Heal *et al.* 1981, Davidson *et al.* 1998, Janssens *et al.* 2003). Soil respiration from soils with different soil textures and different clay contents responds differently to soil moisture since water logging occurs at different moisture contents depending on pore size (Heal *et al.* 1981, Davidson *et al.* 1998). In a temperate mixed hardwood forest, where some sites had a swampy character, the linear limitation of soil respiration reached zero at about 90% vol. (Davidson *et al.* 1998) and in Douglas-fir stand at Vancouver Island, Canada, zero respiration was reached at approximately 35% vol. (Jassal *et al.* 2005). For the different ecosystems in Simpevarp, this limit was reached between these values, at 45% to 60% vol.

Even if  $R_{\text{soil}}$  was reduced by soil moisture, it was not totally inhibited. The main explanation for this is that soil moisture measurements were made in the humus layer at the soil surface whereas soil respiration also originates from the deeper parts of the soil, where other soil moisture conditions exist. With regard to spruce, it would appear that some other factors were limiting soil respiration in the lower soil moisture ranges, while it was soil moisture that was the limiting factor above 50% vol. (Fig. 1).

### Annual soil respiration

Annual  $R_{\text{soil}}$  differed between the ecosystems; tests with  $R_{\text{soil}}$  against different characteristics of the ecosystems could not significantly explain these differences since too few ecosystems were studied. Between annual  $R_{\text{soil}}$  of the forest ecosystems and the age of the forests, a trend relationship could be seen though (cubic regression:  $F = 84.35$ ,  $p = 0.077$ ,  $R^2 = 99.4\%$ ). This means that  $R_{\text{soil}}$  was low in young and old forest ecosystems and high in between. This is the same relationship that age of a forest has to NPP (Gower *et al.* 1996, Smith and Long 2001, Binkley *et al.* 2002, Kashian *et al.* 2005) and according to Janssens *et al.* (2001b); NPP is the main factor to determine soil respiration.

A trend relationship was also seen between the amount of litter and  $R_{\text{soil}}$  (S curve:  $F = 15.51$ ,  $p = \text{value } 0.059$ ,  $R^2 = 88.6\%$ ). It was a negative relationship, i.e. the ecosystems with most litter had the lowest  $R_{\text{soil}}$  estimates. The reason for this could be that the litter measurements were taken up in autumn (Löfgren 2005), before the arrival of new litter. The ecosystem with highest  $R_{\text{soil}}$  had already decomposed last year's litter while the ecosystems with low  $R_{\text{soil}}$  had more litter left. Another explanation could be the quality of litter; it might be that the litter is harder to decompose in the ecosystems with much litter.

The annual  $R_{\text{soil}}$  estimates of all ecosystems but oak 2 were larger than the estimated mean for coniferous forests, deciduous forests and meadows; for coniferous forests the mean is  $1.2 \text{ kg CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$  and for the temperate forests it is  $2.4 \text{ kg CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$  (Raisch and Schlesinger 1992). For grasslands most studies have

reported soil respiration values between  $1.0\text{--}2.77 \text{ kg CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ , which is lower than the  $R_{\text{soil}}$  estimate for meadows (Maljanen *et al.* 2001, Suyker and Verma 2001, Flanagan *et al.* 2002, Suyker *et al.* 2003). Other studies have also shown soil respiration well above these estimated mean, (Davidson *et al.* 1998, Lindroth *et al.* 1998, Law *et al.* 1999b, Granier *et al.* 2000, Morén and Lindroth 2000, Rayment and Jarvis 2000, Bolstad *et al.* 2004, Novick *et al.* 2004), i.e. the values found in this study are in the upper range of soil respiration estimates but still not exceptionally high.

An explanation as to why the coniferous forests have larger soil respiration than the estimated mean could be that Simpevarp is situated further south than the ecosystems examined by Raisch and Schlessinger (1992). Lindroth *et al.* (1998) explained their high soil respiration values with climate variables; the temperature was high and soil moisture was low during periods of large soil respiration. Another explanation could be that the forests of Simpevarp are managed, and at least the spruce forest has recently been ditched.

Other explanations to the large values could be in the measurement technique used: the closed chamber technique. Pumpanen *et al.* (2004) showed in a comparison between different chambers against known amount of  $\text{CO}_2$  fluxes that a SRC-1 chamber from PP-systems estimated the soil  $\text{CO}_2$  fluxes with between 0.86 and 1.33 of the reference soil C efflux, depending on which sand and which soil moisture that the measurements were done on and if collars were used or not. When no collars were used, as in this study, the overestimation was on average 1.05. No tests were done with a CPY-2 chamber though. The problem with the closed chamber technique is that the chamber always affects the soil that the measurements are done on (Davidson *et al.* 2002). First, since the concentration of  $\text{CO}_2$  in the chamber is altered and this affects the concentration gradient from the soil and secondly since pressure anomalies caused by circulating gases or by cooling or warming of chamber air affects the gas exchanges (Davidson *et al.* 2002).

A problem with the evaluation of modelled  $R_{\text{soil}}$  was that relatively few measurements were available. The same  $R_{\text{soil}}$  measurements that were

used in the model were used to evaluate it; ideally the data should have been separated in two parts, one that was used for model estimation and one for the model evaluation. Soil respiration varies over the seasons because of differences in the amount of living biomass, amount of roots, water availability, litter quality and depth of active soil layer (Rayment and Jarvis 2000, Strömberg 2001) and if there had been more data, the season could have been separated into narrower periods.

### Effect of GPP on soil C effluxes

No photosynthesis significantly different from zero was found for the ground vegetation in the forest ecosystems of Simpevarp. In spruce, there was almost no ground vegetation and in oak 2, ground vegetation existed only during spring but disappeared after the development of canopy. For the other forest ecosystems, there was sparse ground vegetation but the amount of C taken up by it was too small to be statistically detectable. Photosynthesis by ground vegetation naturally depends on the structure of the ground vegetation, which then depends on the type of forest. It is also dependent on other factors such as soil moisture, temperature and radiation (Baldocchi *et al.* 1997, Kelliher *et al.* 1999). Some studies indicated that the uptake of CO<sub>2</sub> by the forest floor vegetation can be a significant part of the soil C effluxes (Morén and Lindroth 2000, Widén 2002) while in other studies it was negligible (Baldocchi *et al.* 1997, Kelliher *et al.* 1999).

### Effect of PAR, temperature and soil moisture on ground GPP in meadow

In the meadow, GPP was saturated at 0.909 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>, which is in the same range as in several other studies. Valentini *et al.* (1995) found for a California grassland that light saturation occurred approximately between 0.48 and 1.11 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>, for plants with sun characteristic leaves. Rothstein and Zak (2001) found a levelling off between 0.61 and 2.43 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> and for a grassland and barley fields in Finland, Maljanen *et al.* (2001) found

that maximum uptake of CO<sub>2</sub> was between 0.4 and 1.0 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>.

The average quantum efficiency over the growing season was 0.019 mol CO<sub>2</sub> (mol photons)<sup>-1</sup>, which is similar to Flanagan *et al.* (2002) and Ruimy *et al.* (1994), with quantum efficiencies between 0.018 and 0.025 and between 0.007 and 0.036, respectively.

Former studies showed that photosynthesis increases exponentially at lower temperatures to an optimum after which it starts to decrease (Wang *et al.* 1996, Cannell and Thornley 1998, Lankreijer 1998). Many studies used the Arrhenius function of temperature to show this relationship, whereas Cannell and Thornley (1998) used a cubic regression since it has the same shape but is more mathematically transparent. In this study, the cubic regression was chosen since it is easier for the calculation of the standard deviations. The downside of the cubic regression is that the underlying processes cannot be interpreted.

No significant effect of soil moisture on GPP in the humus layer could be seen. Visually, it seemed that soil moisture had an effect on GPP in both dry and wet regions but there were probably too few measurements to detect it statistically. Other studies showed the importance of soil moisture for photosynthesis. Flanagan *et al.* (2002) found that the main environmental factor to control leaf area index of a temperate grassland was soil moisture and Suyker and Verma (2001) showed that NEE was significantly reduced relative to PAR under the influence of soil moisture stress.

### Annual NEE in meadow

The gross uptake of CO<sub>2</sub> by the ground vegetation in meadows (1.81–1.99 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup>) is similar as compared with that reported by other grassland studies with values 1.0–4.45 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup> (Suyker and Verma 2001, Flanagan *et al.* 2002, Suyker *et al.* 2003, Novick *et al.* 2004). Some of these ecosystems showed larger uptake of CO<sub>2</sub>, but this can be explained by the fact that they are situated further south where the growing season is longer. The NEE of 1.39–2.41 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup> shows that there was a loss of C from meadows to the atmosphere. This is a large loss of C and

the reason could be meadow draining. The measurements were taken within a couple of meters from a ditch and surrounding areas were wet. Recently, it has been shown that soils in England and Wales also lose C and the main explanations are changes in land-use and climate (Bellamy *et al.* 2005).

## Conclusions

We have given further evidence that temperature is a major controlling factor of soil respiration in temperate and boreal ecosystems of the northern hemisphere. Soil moisture also has a limiting effect on soil respiration. We have also shown that GPP of ground vegetation affected soil C effluxes for meadow but it was negligible in relation to soil respiration for the forest ecosystems studied here. Our study also shows that GPP in meadows is controlled by PAR and air temperature.

Further, we have demonstrated that exponential regressions of soil respiration against air and soil temperatures can be used to temporally extrapolate soil respiration. The light response curve of GPP against PAR and the cubic regression of GPP against air temperature could additionally be used to extrapolate GPP throughout the growing season in meadow. Our estimations of annual soil respiration for the ecosystems of Simpevarp were between 2.05 and 4.34 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup>, i.e. high effluxes as compared with those reported in previous studies. Possible explanations for these high values are climatic variables, human impact by management and ditching and errors in the technique used for the estimations of the soil C effluxes. The ground vegetation in the forest ecosystem did not significantly reduce this net flux while in meadow it resulted in an annual uptake of between 1.81 and 1.99 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup>. NEE could hereby be calculated for meadow and annually it lost between 1.39 and 2.41 kg CO<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup>, i.e. a significant loss of C to the atmosphere.

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